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The Periderms of Three North American Conifers
Part 1: Anatomy

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Summary. The anatomy of periderms in three North American conifers are described and compared. The phellems of balsam fir and eastern hemlock consist of tangential bands of thin-walled phellem (TnP) separated by one, or sometimes more, cell layers of thick-walled phellem (TkP). The phellem of white spruce contains tangential bands of TnP and TkP, as well as one to several cell layers of crystalliferous phellem (CP) abaxially adjacent to every TkP zone. The TkP, and to a lesser extent the TnP, are distinctive for each of the three conifers.

The terminations of phellem growth cycles in fir and hemlock are delineated by thickened adaxial suberinic walls in the last-formed layer of TnP cells. In spruce, the adaxial suberinic walls of the last-formed layer of CP cells are thickened. TkP marks the beginning of phellem growth cycles in all three conifers.

TkP cells are "true" suberized phellem cells, not phelloids.

Introduction

The cell was described and named by Robert Hooke in 1665. The "type specimens" for this fundamental structural unit were the phellem (cork) cells of the cork oak (*Quercus suber*) periderm. Despite such auspicious beginnings and the importance of the protecting periderm to the plant, interest in the periderm was soon overshadowed by interest in other plant organs. Research into the periderm still lags, especially at the microstructural and ultrastructural levels.

The primary historical utilization of bark has been as fuel or a source of extractives. Shortages of certain raw materials and an increasing interest in conservation and renewable resources have recently focused interest on bark. Attempts to use bark in industrial products such as consolidated board (Krahmer, Wellons 1973; Lin 1973; Wellons, Krahmer 1973) and reinforced plastic (Miller et al. 1974) have necessitated

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investigations of its physical properties and anatomy. Most studies have dealt with the bark in general (Chang 1954a; Chattaway 1953) and have usually been associated with species identification (Eremin 1976; Eremin, Raskatov 1974; Fillo 1973; Chang 1954b) and commercial usage. The importance of cellular structure to industrial processing is gradually becoming apparent. For example, the separation of pulverized aspen bark and its pulping properties have been linked to cellular structure (Hossfeld, Kaufert 1957). This and other investigations have suggested that almost all bark physical properties, and therefore processing characteristics and potential commercial utility, are strongly influenced by the cellular structure of the periderms (Howard 1971; Lamb, Marden 1968). The periderm structure is most important in this respect. It defines how the bark will break into chips and what will be the chemical nature of bark chip surfaces.

It therefore seemed desirable to include bark among samples collected for other anatomy projects whenever possible. These reports present a compilation of observations made over several years and will, we hope, contribute to the understanding of the anatomical and ultrastructural construction of conifer periderms.

Materials and Methods

The periderms of white spruce (*Picea glauca* [Moench] Voss), eastern hemlock (*Tsuga canadensis* [L.] Carr.) and balsam fir (*Abies balsamea* [L.] Mill.) were studied. Samples of immature and mature bark, with or without rhytidome formation, were collected from living trees, dry lumber, and stored wood samples. Some material was sectioned freehand, and some fresh spruce bark was freeze microtomed.

Fresh samples of fir and hemlock periderms were processed as follows (Roelofsen 1959):

- untreated
- boiling water (3 days)
- lignin extraction (2 hr; hydrogen peroxide: acetic anhydride 2 : 1 at 60 °C)
- suberin extraction (2 hr; boiling solution of 12 g KOH and 12 ml water made up to 100 ml with ethanol)
- lignin extraction followed by suberin extraction.

Some untreated samples were embedded in paraffin. The rest were acetone dehydrated and embedded in Spurr's resin (Spurr 1969).

Fresh samples of the first periderms of spruce were fixed in Karnovsky's aldehyde mixture (Karnovsky 1965), postfixed with 1 % osmium tetroxide, and resin embedded as above.

Some of these fixed and post-fixed samples were osmium-impregnated by the OTO method (Seligman et al. 1966) and critical-point dried by a Freon procedure (Bomar Co.) for scanning electron microscopy. Thick, paraffin-extracted sections of hemlock and fir were air-dried onto glass squares affixed to stubs and sputter-coated with gold for SEM study.

Paraffin and resin sections of hemlock and fir were stained by a variety of common techniques, while more extensive histochemical staining and extraction procedures were carried out on resin sections of spruce (Roelofsen 1959; Jensen 1962; Johansen 1940; Gurr 1965; Reichert 1952; Frey-Wyssling, Mühlethaler 1965; Feder, O'Brien 1968; Fulcher et al. 1976; Eurenius, Jarksär 1970; Wise et al. 1946).

Ultrathin sections of all species were stained with uranyl acetate and/or lead citrate, 1 % potassium permanganate, 1 % potassium permanganate and uranyl acetate (1 : 1) (Parameswaran et al. 1976), or extracted with sodium methoxide (Eurenius, Jarksär 1970) and shadowed with platinum-paladium. Additionally some ultrathin sections of spruce were extracted with sodium chlorite (Wise et al. 1946) for 45 min. prior to the above treatments.

The following equipment was used: an American Optical sliding microtome equipped with a freezing stage; Reichert Zetopan microscopes having an ultraviolet light source and a rotating stage for polarized light microscopy; Reichert OMU-2 and LKB Ultratome ultramicrotomes; a Bomar critical-point drying apparatus; a Philips EM-100 transmission electron microscope; and Cambridge Stereoscan Mark II and Jeol JSM-35 scanning electron microscopes.

Results

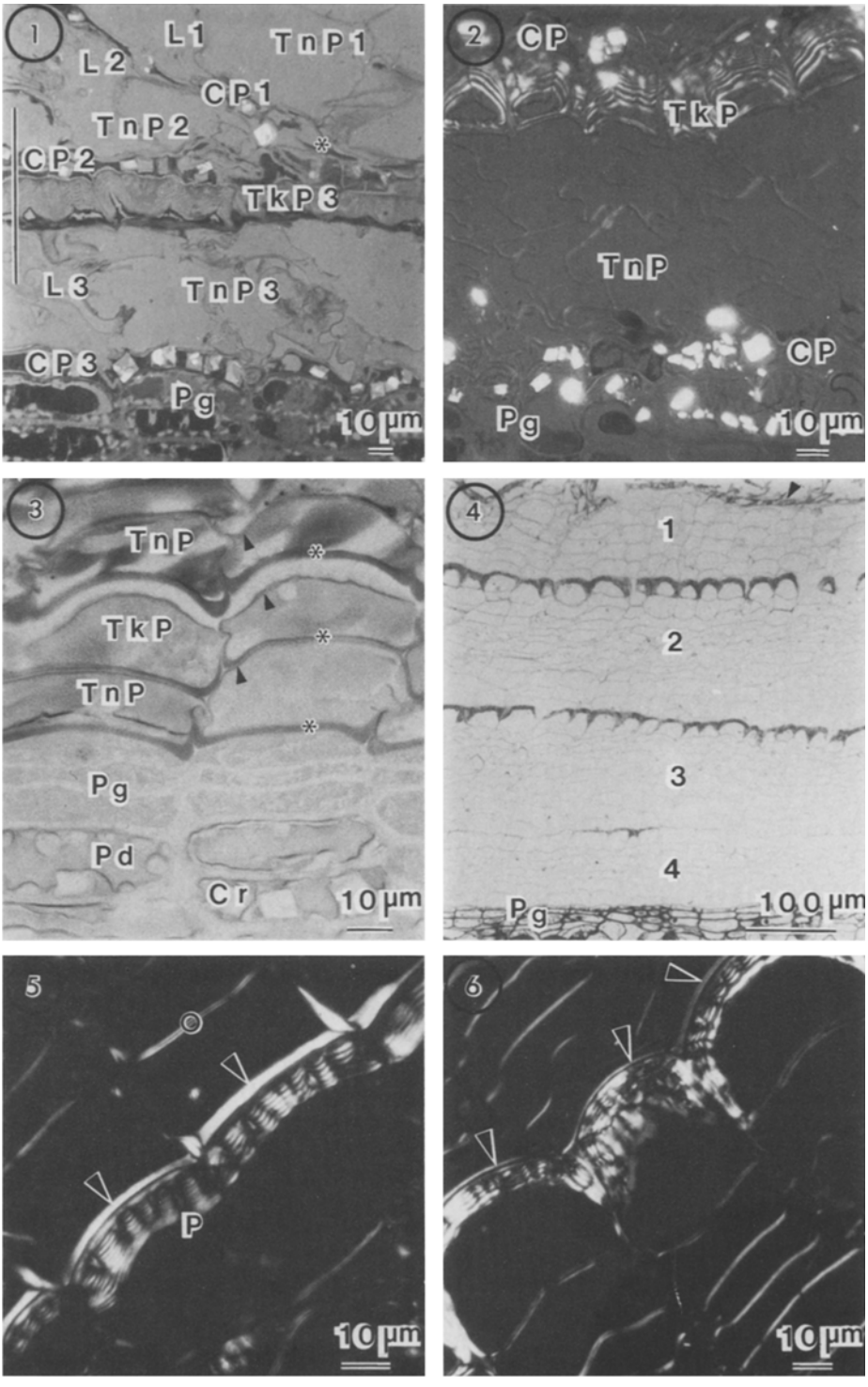
The periderms of white spruce, eastern hemlock, and balsam fir differ in morphological and anatomical features, as well as ontogeny. The existing nomenclature on periderms define the first periderm formed as the first periderm. The periderms formed after the first periderm are the secondary or sequent periderms. Each periderm consists of several cycles of repeating cellular structure. In addition to the first and sequent periderms, the terms wound and pathological periderms are also used in the literature. These periderms are formed to seal wounds or provide pathological protection.

The first periderms of both fir and hemlock are smooth surfaced, but within a few cycles in hemlock it is replaced by sequent periderms. These produce smooth, discoidal scales at first, followed by the thick rhytidome with its deep longitudinal furrows and smooth flat-topped ridges. The first periderm of balsam fir, as in the cork-bark fir (Morgensen 1968), is very long-lived. The tree may be quite old before sequent periderms initiate the formation of a scale bark. Spruce first periderms produce thin, papery phellem scales and have intermediate lifespans. Spruce rhytiodomes, like those of fir, consist of irregularly shaped scales.

Anatomy and Ontogeny

Spruce

Spruce periderms (Figs. 1 and 2) consist of five cell types arranged in centripetal tangential layers: phelloderm (Pd), phellogen (Pg), crystalliferous phellem (CP), thin-walled phellem (TnP), and thick-walled phellem (TkP) (Godkin et al. 1977 and 1978).


1
L1
TnP1
L2
CP1
TnP2
CP2
TkP3
L3
TnP3
CP3
Pg
10µm
2
CP
TkP
TnP
CP
Pg
10µm
3
TnP
TkP
TnP
Pg
Pd
Cr
10µm
4
1
2
3
4
Pg
100µm
5
P
10µm
6
10µm

The first cells created by a newly initiated Pg are usually TnP, although TkP may be formed. A typical growth cycle following dormancy of an existing Pg begins with the production of TkP. Sequent Pgs usually produce 3–4 layers of TkP cells, while first Pgs usually produce one layer. In general, more TkP is formed as the Pg ages and in subsequent sequent periderms. A band of TnP is formed next. Both first and sequent Pgs usually produce 3–4 layers, so that the ratio of TkP to TnP increases as the tree ages. The growth cycle ends with the development of one, sometimes more, layers of CP. A phellem growth increment then consists of TkP, TnP, and CP. One layer of Pd is usually also formed.

Parameswaran et al. (1976) reported that the quantity of spongy cork (TnP) decreases greatly with subsequent sequent periderms in *Picea abies,* and may even not

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Fig. 1. Transverse section of an eastern white spruce first periderm showing portions of three phellem lenses (L_1, L_2, L_3) and the inactive Pg. A lens (e.g. L_3) represents one complete phellem growth cycle, and except at its edges (e.g., only an edge of L_2 is shown) consists of layers of three types of phellem (TkP_3, TnP_3, CP_3). The CP of a younger lens (L_2, CP_2) merges peripherally (asterisk) with the CP of the next older lens (L_1, CP_1). Portions of two lenses (e.g., L_2 and L_3) will exfoliate as a single phellem scale (bracket). Toluidine blue in borax. X358. Bar = 10 μm

Fig. 2. Radial section of an eastern white spruce first periderm having two layers of CP abaxial to the Pg. The multilamellate TkP cellin walls and the CP crystals are brightly birefringent. In comparison with hemlock and fir TkP and TnP, spruce TkP cells tend to have the thickest abaxial walls and smallest lumina, while spruce TnP cells tend to be the most radially expanded. Polarized light. X448. Bar = 10 μm

Fig. 3. Transverse section of a balsam fir sequent periderm. Only a single layer each of TkP and TnP were formed in the last phellem growth cycle. The abaxial cellin walls of the TkP cells are unstained, while the suberinic walls of the TnP cells are densely stained by lipid stains. The adaxial suberinic walls (asterisks) of both TkP and growth-cycle-ending TnP cells are normally thicker than the abaxial walls (arrows) of the same cells. The phellem cell lumina are filled with ergastic materials. Crystals are present only in the Pd. Sudan black B. X660. Bar = 10 μm

Fig. 4. Radial section of an eastern hemlock sequent periderm. Four bands of TnP represent four growth cycles of a periderm which initiated immediately adaxial to an existing periderm. TkP, which marks the beginnings of all but the initial growth cycle (TnP1), occasionally fails to develop thick abaxial walls. A fracture through the Pg (arrow) abscised the phellem of the previous periderm. Potassium permanganate. X130. Bar = 100 μm

Fig. 5. Transverse section through the phellem of a balsam fir sequent periderm. The birefringent cellin wall lamellae of the TkP cells are indented by many pit canals. The birefringent suberinic walls of adjacent TnP cells are separated by thin isotropic common walls (circle). Thick adaxial suberinic walls in the TnP (arrows) mark the end of a phellem growth cycle. Polarized light. X710. Bar = 10 μm

Fig. 6. Radial section through the phellem of an eastern hemlock sequent periderm. The TkP cells are abaxially domed, with the multilamellate cellin thickening extending adaxially along the radial walls. The adaxial suberinic walls of the growth cycle ending TnP cells (arrows) are consistently thinner than their counterparts in balsam fir. Polarized light. X520. Bar = 10 μm

TnP thin walled phellem, TkP thick walled phellem, CP crystalliferous phellem, Pg phellogen, Pd phelloderm, P pit canal, L lens, Cr crystal

be formed. The amount of phlobaphene cork (CP) also increased. These differences from our observations may be species differences, but could be age effects, as our samples did not include trees comparable in age to their material.

The overlapping phellem lenses characterizing the first periderm of spruce appear to arise from spotty activity of the first Pg. The layers of TkP and TnP in a lens decrease in number and taper to an end circumferentially. The TkP ends first (Fig. 1, L_2). The only phellem which is always present and continuous from lens to lens, and probably forms one of several unbroken rings around the stem, is the CP. Comparatively inactive Pg may form CP alone, one layer per growth cycle, so that three or more layers of CP may occur in some interlens areas (Fig. 2). The marginal CP of a new lens always joins with that of adjacent or older lenses (Fig. 1).

Phellem scale exfoliation begins when a radial fissure ruptures the layer of CP near a phellem lens margin (e.g., CP of L_1, Fig. 1). The edge of the phellem sheet curves outwards as the fracture proceeds through the band of TnP under the CP and TkP. The exfoliating phellem scale consists of phellem formed during two growth cycles, as it is a curved sheet of CP and TkP with remnants of TnP on both surfaces (Fig. 1, bracket).

Sequent periderms become active over larger areas, and cut off larger scales of cortex and phloem. The sequent periderms may merge at scale edges in the same manner as do first periderm lenses, or the next Pg may be initiated beneath the previous Pd.

Hemlock and Fir

The periderms of hemlock and fir are composed of four cell types: Pd, Pg, TnP, and TkP. TnP is the first phellem formed by new Pgs (Fig. 4). Subsequently, growth cycles begin with the production of 1–3 layers of TkP, which is followed by 6–12 layers of TnP. As the growth cycle ends, the TnP layer (or layers) adjacent to the Pg develops thick adaxial suberinic walls. The extra thick segments of the inner cell wall layer appears as walls within the cells. They are enclosed by the outer cell wall layers and we will refer to them as "cellin" walls. Their position is described in respect to the central axis of the plant, i.e., abaxial, adaxial, tangential. In the periderms we found they can be present in TkP, TnP and CP cells. They are particularly prominent in fir (Figs. 3, 5). The TnP cells abaxial to the TkP and Pg are always thickened, in contrast to the TkP which occasionally fails to develop thick abaxial cellin walls, particularly in hemlock (Fig. 4). A hemlock or fir phellem growth increment usually consists of TkP, TnP, and adaxially-thickened TnP. Usually a layer of Pd is also formed.

The occurrence and differentiation of TkP in these species is quite variable, as has been previously noted (Chang 1954a; Srivastava 1963; Grozdits, in press), and seems partly age-dependent in that TkP seems to occur more regularly in sequent than in first periderms. However, individual trees and species may vary widely. Patel (1975) has reported that stone cells are only formed in the phellem of radiata pine and Douglas-fir early in the lives of the trees.

First Pg activity may also be spotty in these species as it is in spruce, but activity seems to be greater and of the ring meristem type, similar to that in *Abies alba* (Golinowski 1971). Hemlock first Pgs act the most like ring meristems. A few phellem pockets are formed in hemlock sequent periderms. The TkP, whether fully differentiated or not, and the adjacent adaxially-thickened TnP are circumferentially continuous. Fir first periderms also form some phellem lenses. However, neither species generates exfoliating phellem scales as does spruce.

Rhytidomes

Rhytidome scale exfoliation occurs when bands of TnP in periderms enclose areas of cortex or phloem fracture. The split often runs just abaxial to a band of thickened TkP. In all three species, cells in the first band of TnP (Fig. 4, top band of TnP) formed by the new Pg tend to have thinner, less crumpled walls and less ergastic contents than do cells in TnP formed subsequently. Abscission fractures preferentially occur through this layer, so that the exfoliating scale is bounded on the abaxial surface by a periderm exposing remnants of TnP underlain by either CP and TkP (spruce) or thickened TnP and TkP (fir and hemlock), but bounded on the adaxial surface by remnants of this TnP layer only. Abscission fractures may also occur through secondary phloem sandwiched between two periderms along a dead phellogen (Fig. 4), or even along a TkP layer. Bark flakes in *Pinus nigra* (Patel 1975) also arise from fractures through a layer of thin-walled phellem lacking dark contents, or less frequently, through the dead phloem. In all three conifers the ruptured TnP ultimately exposes a heavily suberized sheet supported by the mechanically strong TkP, a combination which should offer the most protection for the tree. These natural fracture zones are important when bark is industrially processed. When ground, bark fractures along the periderm into periderm-bounded particles resistant to further treatment along the periderms. Ultimately, the periderms separate as sheets from the other rhytidome tissues. The sheets of TkP are particularly persistent (Godkin et al. 1978).

Periderm Cells

The overall shapes and dimensions of the periderm cells of the three species coincided with previous documentation (Chang 1954a; Chang 1954b; Esau 1967; Grozdits, in press).

Phellogen and Phelloderm

The Pg cells have thin walls which are primary in nature. The walls of the Pd cells thicken progressively with adaxial distance from the Pg (Figs. 1, 3). They are expanded

primary walls (Grozdits, in press). Both Pg and Pd walls are characterized by prominent, primarily radial, simple pits, and by positive tests of cellulose, hemicellulose, and pectins. The middle lamella and cell corner regions are particularly rich in pectins. We found no evidence for lignin until the periderm had been isolated by a sequent periderm. Since lignification is not known in dead tissues, it is presumed the lignin stains were detecting polyphenols formed during the phase of dying of the periderm.

Older Pd cells may differentiate into crystal-containing cells conforming to published descriptions of crystal cells (Wattendorff, Schmid 1973; Wattendorff 1969). The only diagnostically significant differences between species in the structures of the Pgs or Pds were the frequency and appearance of Pd crystal cells, and the types of crystals present. In spruce and fir these dead cells are full of dense amorphous tannin deposits in which one to several cubic or rhombic crystals are embedded (Fig. 3). The crystals have suberinic sheaths continuous at some point with a thin suberinic layer lining the lumen. These cells, particularly in fir, may form almost continuous tangential rows. In hemlock the crystal cells contain less tannin, occur more sporadically, and contain long, rectangular crystals with bluntly pointed ends.

Thin-walled Phellem

The thin-walled phellem cells have similar wall characteristics in all three species. The common wall, shared by two cells, is a lignified cellulose membrane containing some phenolic material. It is sheathed by thicker suberinic cell wall layer. Following boiling water extraction, the suberinic layers lacked their usual birefringence and were wrinkled into ridges and folds. The suberinic layers are of similar thicknesses in all species and are of uniform thickness, with the exception of the growth-cycle-marking, adaxial, tangential walls of fir and hemlock TnP (Figs. 3, 5, 6). These adaxial walls are highly birefringent, and stain intensely for lipidic substances (Figs. 3, 5, 6). In hemlock (Fig. 6) the adaxial walls are about twice the usual wall thickness, while in fir (Fig. 5) they can be many times thicker. In some fir periderms most adaxial walls are thickened to some degree.

The first periderm of hemlock produces unique TnP. Both adaxial and abaxial tangential walls are thickened, the cells contain many small crystals (rare in sequent TnP), as well as brownish deposits rather than the reddish-purple, leachable tannins which characteristically fill TnP cells in sequent periderms (Fig. 4). The deposits in fir TnP are generally yellowish-brown or golden, and whether filling or merely lining the lumina, they are not readily leachable (Fig. 3). The TnP cells of spruce rarely contain more than cytoplasmic debris.

The CP of spruce is really a tubular type of TnP. The suberinic walls tend to be thicker than those of the adjacent TnP, especially the thick growth-cycle-ending, adaxial, tangential walls. They are highly birefringent and stain densely for lipidic and mildly for phenolic substances (Godkin et al. 1977). Cell lumina are filled with

yellowish-to reddish-brown osmiophilic tannins in which several cubic or rhombic crystals, probably calcium oxalate, may be embedded (Figs. 1 and 2).

All TnP cells lack open pits when viewed in the light microscope, and tend to have convoluted radial walls.

Thick-walled Phellem

The unthickened radial walls of TkP cells are also often convoluted. Light microscopically visible pits are absent from all but the abaxial walls. The TkP cells of the three conifers are characterized by greatly thickened abaxial tangential walls, yet are morphologically distinct. The abaxial walls are thickened by many alternating thick and thin cellulose lamellae, have a relatively low lignin content in comparison with the compound middle lamella and cell corner regions, and stain slightly for phenolics. The blind tubular channels of many simple pits penetrate and deform the lamellae, creating a scalloped effect (Godkin et al. 1978).

The TkP cells of spruce (Figs. 1 and 2) are the most tubular among the three species, having about the same radial thickness as the CP cells. When fully developed, the multilamellate secondary wall occupies half or more of the cell. The lamellae tend to run around the corners slightly and taper adaxially along the short radial walls, giving the thick wall a mild crescent shape. The radial walls and adaxial tangential walls are characteristically only slightly thickened, but are commonly thicker where several TkP layers abut than in an isolated layer. The narrow lumina are often completely filled with tanniferous material like that in the CP.

Fir TkP (Figs. 3, 5) is quite similar to spruce TkP in appearance, but the thickening lamellae tend to end more abruptly at the radial walls. Cellular dimensions and contents are similar to those of the adjacent TnP.

Hemlock TkP (Figs. 4, 6) also has dimensions and contents similar to its TnP but usually appears more expanded radially. The abaxial wall thickening is distinctively different from that of spruce and fir. The cellin thickening tends to appear thinner, tapers adaxially along the radial walls, and usually extends slightly around the adaxial corners (Figs. 4, 6). The remainder of the adaxial wall is usually only slightly thickened. The abaxial cell corners are rounded and the radial walls only slightly thinner than the abaxial wall. In transverse and radial sections the thickening is dome-shaped, enclosing a half-moon lumen (Grozdits, in press).

The innermost cell wall layers in the TkP cells of fir and hemlock seem the same in structure and composition as, but are thinner than, the suberinic TnP walls (Fig. 3). These lumen-lining layers are generally thinnest abaxially. Pronounced adaxial thickening like that occurring in the TnP usually occurs only when a layer of TkP overlies another TkP layer or the Pg. Spruce TkP cells are light microscopically devoid of suberinic layers. However, the electron microscope reveals a very thin, almost transparent, non-osmiophilic, lamella lining the lumina.

Discussion

First phellogen activity in all three species seems to be slow and spotty, with hemlock Pg appearing to be the most uniformly active. Arzee, et al. (1970) have reported similar Pg activity in acacia, an indication that this activity pattern may be of general occurrence. Similarly, observations of radiata pine (Sands 1975) agree with our impression of greater activity by sequent phellogens.

The exfoliation of scales by the fracture of a band of TnP is undoubtedly related to the different types of phellem and their layering (Esau 1967; Patel 1975). Von Höhnel (1877) described the TkP cells of certain periderms, including those of *Picea excelsa,* as "active abscissphelloids". He described the thick-walled lignified phelloids as being special cells interspersed between the layers of true (suberized) phellem cells to facilitate exfoliation. Hygroscopically-induced flexure of the absciss-phelloids was hypothesized to cause rupturing of the thin radial walls of the TnP cells adaxial to the layer of absciss-phelloids. Our observations support this explanation.

The existence of bands of thick-walled lignified cells in the phellem of certain species has been known at least since von Höhnel described them in 1877. However, their ontogenetic status in the Phellem as the first cells formed by a re-activated phellogen seems to be previously unreported. Only a few reports mention phellem growth increments. In 1968, Morgensen stated that phellem increments of cork bark fir were separated by "rows of cells with thick sclerified outer tangential walls". Later, Patel (1975) noted that "growth zones" in Douglas-fir phellem were sometimes separated by a line of slightly thickened tangential cell walls, but did not say whether these were sclerified or suberized walls. Neither author indicated whether the thick cell walls began or ended a growth increment.

The commonly unilateral cellin wall thickenings of the TkP cells are better documented. In some cases the adaxial walls are thickened (Srivastava 1966; Haberlandt 1914; von Höhnel 1877); in others the abaxial walls are thickest (Srivastava 1966; Morgensen 1968; Litvay, Krahmer 1977; Parameswaran et al. 1976; Grozdits, in press). Except in the case of eastern hemlock (Grozdits, in press), the thin suberinic walls of these TkP cells have remained undetected. As a result, these cells are commonly labelled "phelloids", supposedly being devoid of suberin and therefore not "true" phellem cells. We now know that TkP cells of fir, hemlock and spruce do have suberinic wall layers, and the phelloid concept is invalid for them.

We have found no evidence to support Chang's (1954a) view that TkP originates from the Pd of a periderm isolated by a new Pg initiated immediately adaxial to its Pd. Our observations all indicate that TkP is a Pg product and is genuine phellem. Parameswaran et al. (1976) have also concluded that the "sclerotic phelloids" (TkP) of *Picea abies* periderm, which is similar to the periderm of *Picea glauca,* are obviously products of the Pg. Others believe that the thick-walled cells in pine (Patel 1975) and Douglas-fir (Grillos, Smith 1959) phellems are a special kind of phellem.

The lignification of the common walls between TnP cells is well known (Roelofsen 1959; von Höhnel 1877; Golinowski 1971) but is not always evident (Srivastava, 1966;

Arzee et al. 1970). Some phenolics have been found previously in the common walls of Douglas-fir cork cells (Arzee et al. 1970). Unilateral thickening of the suberinic TnP walls, such as we have recorded, has been previously reported only by Haberlandt (1914), who mentioned that the suberin lamella of the abaxial wall is sometimes thicker than that of the adaxial. The adaxial suberinic wall thickenings ending each phellem growth increment were prominently characteristic of our material, but we have been unable to find any previous mention of suberinic wall thickenings associated with the phellem growth cycle.

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